Whose poop is this? The case of the Late Cretaceous coprolite with a clearly identified producer and the feeding habit of *Ptychodus*

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Abstract

Background. Coprolites, i. e. fossilized fecies, are an important source of knowledge on the diet and food processing mechanisms in fossil record. Here we examine a shark coprolite from Opole Cretaceous deposits to describe its producer and producer's feeding habit.
Methods. To achieve that, coprolite was scanned using micro computed tomography to show the arrangement of the inclusions (remnants of the producer's meal). In addition a cross-section was examined under SEM/EDS to analyze inclusions microstructure and chemical composition.
Results. Analysis showed numerous inclusions in various shapes. Some of them can be described as possibly brachiopod, and least one foraminiferan shell can be determined. SEM photographs confirms that most of inclusions are fragments of brachiopod shells.
Conclusions. The producer of the coprolite can be determined as the shark *Ptychodus* ~~shark~~. Due to the fact that there are~~is~~ no bivalve (inoceramid) shells in the coprolite mass, but foraminifera remains can be recognized among~~long~~ numerous brachiopod shells, a durophagous-filter feeding habit can be proposed for *Ptychodus* instead of typical durophagous habit.

Introduction

Coprolites, i.e. fossilized faeces, together with cololites (intestine contents), gastroliths (stomach, or gizzard, stones) and regurgitates (orally expelled masses) make up the group of ichnofossils known as bromalites. These are informative for establishing the diet and food processing style. The major caveat is the uncertainty concerning the specific producer of this kind of fossils. Sometimes, the co-occurrence within the same strata of bones and fossil faeces, and specific features of the animal linking the coprolite and skeletal material (e.g. size, purported died), can be used as means to pinpoint, with a certain level of certainty, the most likely producer. These were done for the Late Triassic site of Krasiej6w in the Opole area, where small coprolites, containing insect remains,

Commented [AH1]: I would use the term consumulites that includes all material preserved within the digestive tract (e.g., Hunt, A. P. and Lucas, S. G., 2021, The ichnology of vertebrate consumption: Dentalites, gastroliths and bromalites: New Mexico Museum of Natural History and Science Bulletin 87, 215 p.)

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were identified as a product of a co-occurring dinosauromorph *Silesaurus opolensis*, with the main reasoning based on body sizes and possible diets of the skeletally identified fauna at locality (Qvarnstrom et al. 2017, 2019, 2021). The discussion there, however, did not take into account taxa identified only from teeth~~dentally-only identified taxa~~. Here the producer of the Late Cretaceous coprolite from Opole is identified to the genus ~~without a doubt~~, based on the diet preferences of co-occurring ichthyofauna.

Shark teeth and coprolites are a common find in Late Cretaceous deposits, including the Turonian-Coniacian of Opole area. Skeletal fossils consist mainly of isolated teeth, with few finds of an associated dentition or even a single vertebrae. Nied¿łwiedzki (2005) and Nied¿łwiedzki & Kalina (2003) are the only authors that ~~in recent years~~ have studied ~~dealt with~~ the shark fauna of the Opole area in recent years.

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Nied¿łwiedzki & Kalina (2003) described from Opole the following taxa: *Ptychodus latissimus*, *P. mammillaris*, *P. polygyrus*, *Squalicorax* sp., *Scapanorhynchus raphiodon* and *Paranomotodon angustidens*. Nied¿łwiedzki (2005) listed jointly taxa from Opole and Sudetes area. Apart from those mentioned above, other taxa said to be common were *Cretoxyrhina mantelli*, *Cretolamna appendiculata*, *Squalicorax falcatus* and *Odontaspis subulate*, while rare finds included *Hexanchus microdon*, *Synechodus ma}or* and *Hybodus dentalus*. In a popular book (Yazykova (ed.) 2017, 2019, 2022), Nied¿łwiedzki confirms the presence specifically in the Opole area of *Squalicorax falcatus*, *Cretolamna appendiculata*, *Cretoxyrhina mantelli* and *Odontaspis subulata*. These works are supplemented by the collecting efforts of the current authors, whos~~ere a~~ rich collection preserves *Squalicorax falcatus* and other lamniforms, *Ptychodus* spp., as well as a single find of hexanchiform.

As for coprolites, spiral shark faeces are especially common in clayey marls. Their general presence was noted by one of us in an MSc Thesis (Mazurek, 2008), an occurrence later cited by Hunt et al. (2015).

Materials & Methods

A shark coprolite from Odra II quarry was collected during the summer digging camp in 2020. It is housed at University of Opole (col. no. IBUO-DMKOPRO1). Fieldworks w~~ere~~as possible due to the legal agreement between the quarry owner (Cement Factory "Odra" and European Centre of Palaeontology, University of Opole) from 24.05.2017.

The c~~C~~oprolite has a typical size (22 mm in length, however, it is incomplete, the whole coprolite could be at least two times larger) and the spiral shape (Fig. 2E) of a chondrichthyan coprolite. As the specimen is broken, some dark infillings are visible within grey phosphatic mass ~~some dark infillings are visible~~ on the cross-section (Fig. 1). To decide what kind of infilling they are, the specimen was analysed with a~~scanned under~~ micro CT scanner SkyScan 1273 in Bruker Laboratory in Kontich, Belgium. Obtained data were presented using DataViewer (for multiple cross sections in three directions) and CTVox (for the presentation of the 3D orientation of infillings) software.

For chemical identification of the infilling, the surface of the broken part (cross-section) was polished with grinding powder. The obtained polished surface was examined under Scanning

Electron Microscope TM 3000 with secondary electrons as well as with the use of Energy-Dispersive X-ray Spectroscopy.

Odra II quarry is a working quarry within the city of Opole (southern Poland). The succession exposed starts with clayey marls (Middle Turonian *Inoceramus apicalis* Zone) and proceeds with limy marlstones (Middle Turonian *I. lamarcki* Zone to lowermost part of Upper Turonian *I. costellatus* Zone), and ends with marly limestones (*I. costellatus* Zone). This sequence of strata forms part of a one transgression-regression megacycle (Cenomanian-?Santonian) that represents the Cretaceous strata of the so-called Opole Trough (Jagt-Yazykova et al. 2022). The biota preserved is numerous, and consists of ichnofossils, sponges, inoceramids and other bivalves, brachiopods, fish remains, cephalopods, echinoderms, crustaceans, cnidarians, shark coprolites, land flora and rare marine reptiles. The specimen studied comes from the clayey marls (Middle Turonian: *I. apicalis* Zone).

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Results

MicroCT scan reveals numerous infillings of density different from than phosphatic background of the coprolite mass (Fig. 2, 3). Most of the shapes are irregular, many being boat-shaped. Some of them can be recognized and assigned to certain groups of animals, specifically micro morphic brachiopods and foraminifera. Two unspecified shells/tests have been observed under higher magnification under SEM. Both inclusions (Fig. 4) show the walls consisting of horizontal lamellae. No vertical elements are present, which would be expected in the case of an inoceramid prismatic layer (e. g. Jimenez-Berrocoso et al., 2006). No macroscopic chunks of large bivalves are present either. The microstructure is more reminiscent of inpuncate brachiopod shells. Regardless, some inclusions can be firmly identified~~classified~~ as brachiopods and forams (Fig. 2, 3), while inoceramids (the supposed food source of *Ptychodus*) are lacking entirely.
In the EDS analysis, the main elements are: Ca, O, C and P (Fig. 4).

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Discussion

Irregular and boat-shaped infilling creates a similar pattern to the infillings in coprolites of durophagous fishes from the Middle Triassic (Antczak et al., 2020). EDS signature suggests that these are elements made of calcium carbonate (while the matrix of the coprolite possesses a phosphatic character). This means that the analysed coprolite was produced not by a piscivorous shark but rather by species feeding on invertebrates with calcareous shells. The assignment of some of the infillings to brachiopods suggests that the producer was feeding at the bottom of the sea (nektobenthonic) instead of in open water~~s~~ (nektonic). In addition, tests of calcareous foraminifera can be recognized, similar to genera *Lenticulina* or *Gavelinella* (KCapciEski & Teisseyre, 1981) which are bottom-dwelling taxa, probably swallowed accidentally together with the sediment and a brachiopod laying on the bottom of the sea.
In the Turonian of Opole, several shark species could~~an~~ produce coprolites of this size. The known taxa are *Cretoxyrinha, Hexanchus, Squalicorax* and *Ptychodus*. Among them, only the last one is the only one commonly described as durophagous based on tooth morphology (Shimada et al., 2009, 2010)

(Fig. 5). Niedżłwiedzki and Kalina (2003) identified from the Opole Cretaceous three taxa of *Ptychodus*. Apart from isolated teeth, the Opole Cretaceous also yielded two sets of teeth: one is deposited at the University of WrocŁaw, while the other is in a museum of the University of Opole. Similar finds are known for several taxa worldwide (Amadori et al., 2019; Hamm, 2017), with partial skeletons or skulls much rarer (Shimada et al., 2009, 2010). This means that the producer of the coprolite can be specifically identified to the mentioned genus. However, the lack of inoceramid shell fragments within the coprolite is puzzling, and one alternative that can be considered is the *Ptychodus*, contrary to current opinions, was not a durophagous taxon, but rather a filter feeder, with water moving between the ridges of the teeth. Such an elaborated ornamentation as present on the teeth of *Ptychodus* is lacking in many other durophagous taxa, including among others: fishes (e. g. Purnell and Darras, 2015), placodonts (Pommery et al., 2021) and mosasaurs (Leblanc et al., 2019), the teeth are usually restricted to the outer edge of the jaws, and supposed shark dentalites~~bite marks~~ on inoceramids are surprisingly rare in the literature ~~known to us~~ (e.g., Kauffman, 1972; Hunt and Lucas, 2021, table A.5).

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Commented [AH9]: Why do you think a filter feeder would have large bulbous teeth? What would be the function.

Conclusions

MicroCT scan and EDS analysis show that coprolite collected in the Turonian deposits of Odra II quarry in Opole, southern Poland is filled with shell fragments. Inclusions can be identified as remains of small brachiopods (and occasionally foraminifers). Such content allows us to identify the producer of the coprolite to the genus level as *Ptychodus*, the only large fish that fed on shell-covered invertebrates in the Late Cretaceous deposits of this locality. A diet composed of benthonic forams and small-sized brachiopods suggests that *Ptychodus* might have been a filter feeder and not a typical durophagous fish as there is no evidence of preying on abundant large inoceramids.

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Figure 1

Analysed coprolite.

(A) Lateral view. (B) Cross-section.

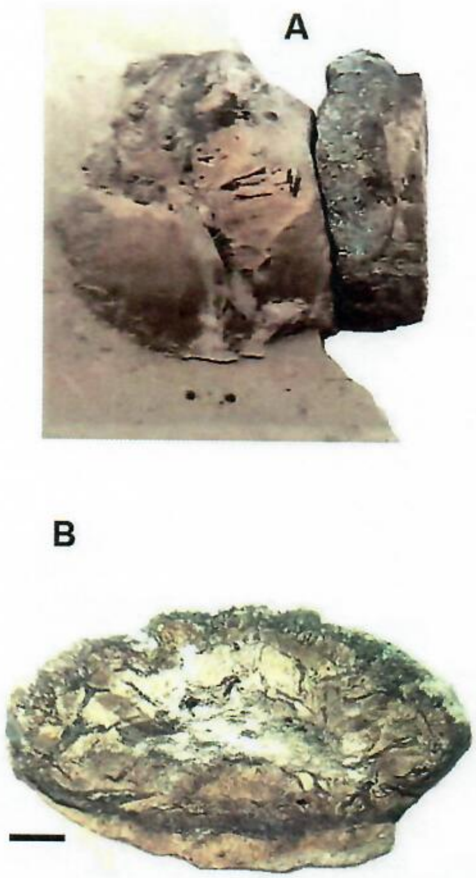


Figure 2

MicroCT scan of the coprolite.

(A-D) Infiûllings in the coprolite mass 3 3D model. (E-F) Longitudinal cross-section. b 3 brachiopod shell, f 3 foram shell.

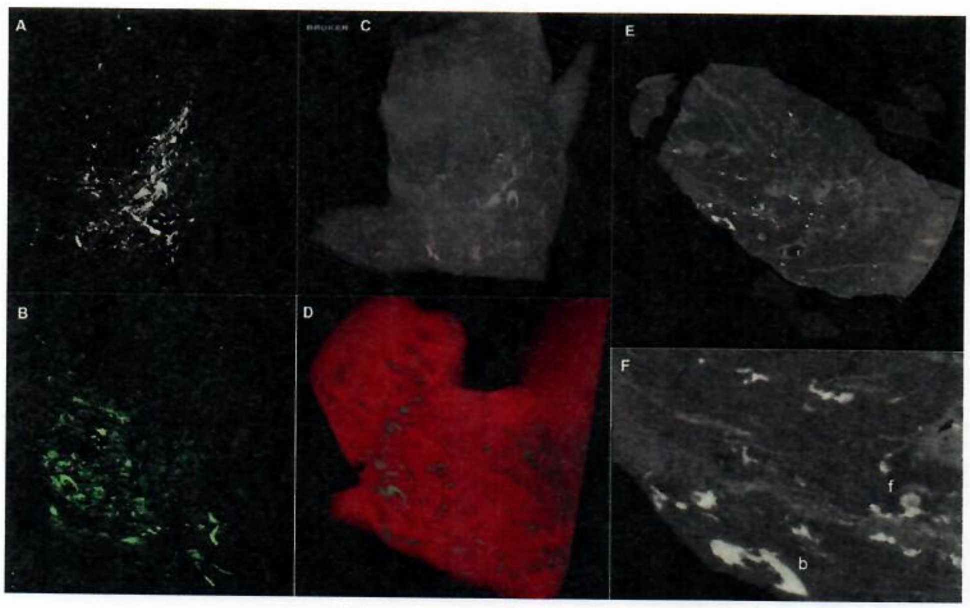


Figure 3

Cross-sections of the analysed coprolite.

(A, C, D) Cross-sections in 3 directions. (B) Magnifiûcation of the example of indeterminate. shell fragment.

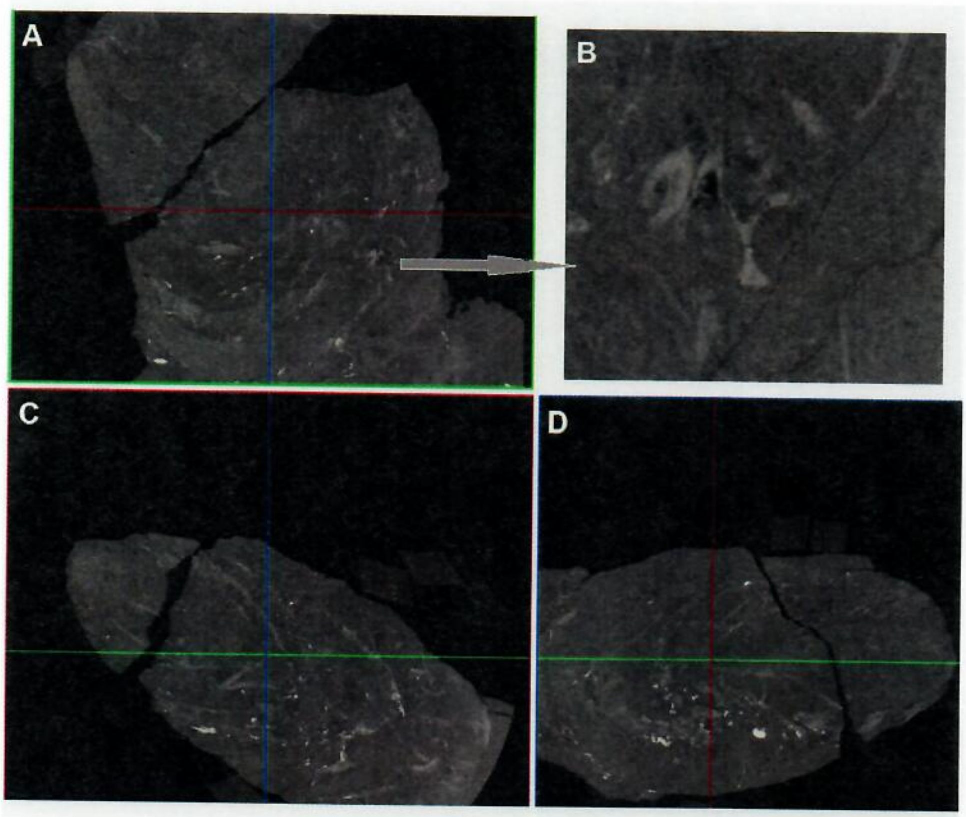
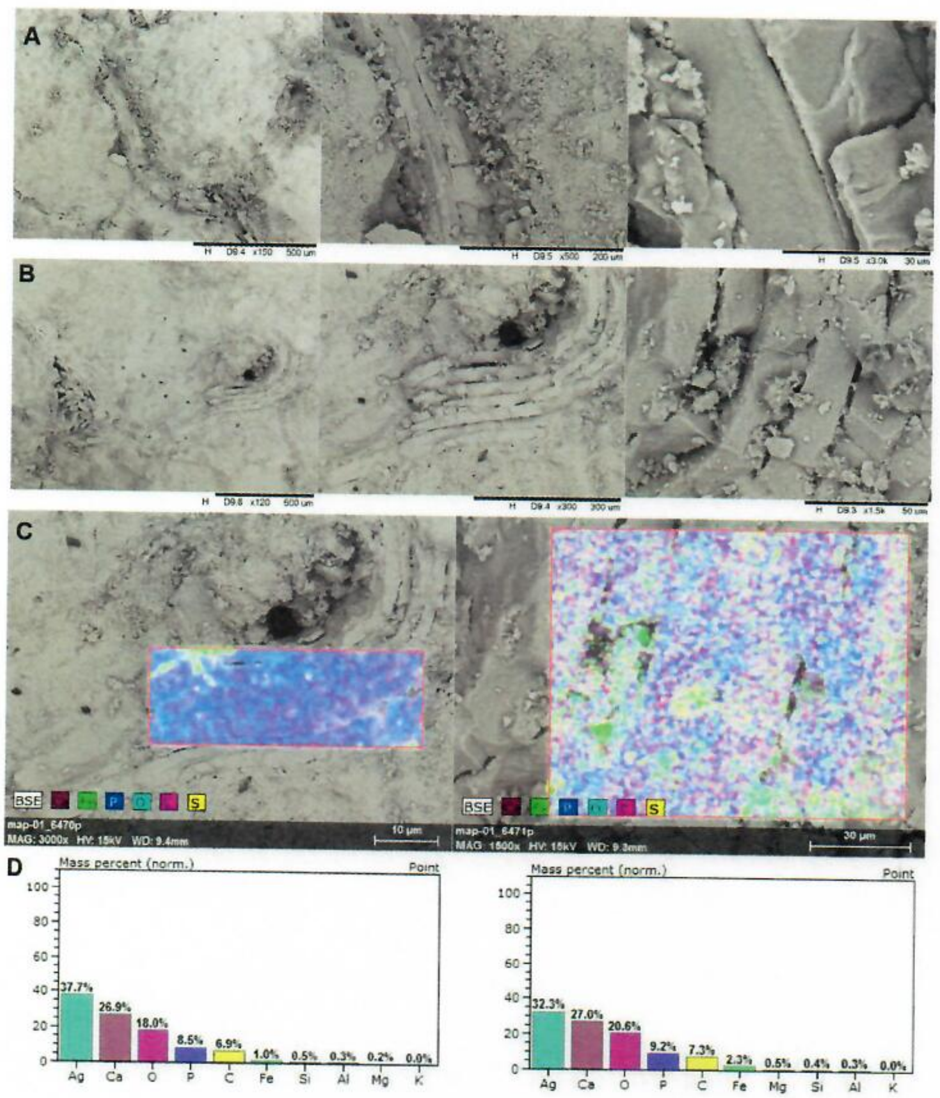


Figure 4

EDS analysis.

(A, B) Brachiopod shell fragments. (C) EDS surface analysis. (D) Mass percentage result.


A
B
C
BSE
map-01_6470p
MAG: 3000x HV: 15kV WD: 9.4mm
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map-01_6471p
MAG: 1500x HV: 15kV WD: 9.3mm
30 µm
D
Mass percent (norm.)
Point
37.7% 26.9% 18.0% 8.5% 6.9% 1.0% 0.5% 0.3% 0.2% 0.0%
Ag Ca O P C Fe Si Al Mg K
Mass percent (norm.)
Point
32.3% 27.0% 20.6% 9.2% 7.3% 2.3% 0.5% 0.4% 0.3% 0.0%
Ag Ca O P C Fe Mg Si Al K

Figure 5

Ptychodus reconstruction

(Drawing by Jakub Kowalski)